

## Positional Behavior and Vertebral Morphology in Atelines and Cebines

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**KEY WORDS** platyrrhine; lumbar; locomotion; posture

**ABSTRACT** Atelines are of particular interest to primate evolutionary studies because they converge with hominoids in postcranial anatomy, including the vertebral column. Currently, our understanding of ateline vertebral morphology is limited to mainly qualitative descriptions and functional interpretations based on general categories of positional behavior. Even less is known about the vertebrae of other platyrrhines. This study more closely examines vertebral form and function in atelines and cebines by combining direct field observations of axial postures and movements, assessments of spinal loading regimes, and a detailed vertebral morphometric analysis. Field observations (Corcovado, Costa Rica) on *Ateles geoffroyi*, *Alouatta palliata*, *Cebus capucinus*, and *Saimiri oerstedii* were quantified in conjunction with a morphometric analysis of ateline and cebine lumbar vertebrae. *Hylobates* was also included for comparison.

Compared to *Cebus* and *Saimiri*, atelines engage more frequently in postures and locomotor behaviors that induce pronounced bending loads on the spine. All atelines share lumbar adaptations for resisting bending, including ventrodorsally elongated vertebral bodies and perpendicularly oriented transverse processes. Among atelines, lumbar region lengths and vertebral bodies are shortest in *Ateles* and *Brachyteles*, longest in *Alouatta* (resembling *Cebus*), and intermediate in *Lagothrix*. Compared to *Cebus* and all atelines, *Saimiri* has a relatively longer lumbar region, longer and less ventrodorsally expanded vertebral bodies, and more ventrally oriented transverse processes. These features accentuate bending loads, but increase the sagittal flexibility required for leaping. Vertebral convergence between hylobatids and atelines is more readily interpretable as a product of shared spinal loading patterns than shared positional behaviors. *Am J Phys Anthropol* 105:333-354, 1998. © 1998 Wiley-Liss, Inc.

As a key functional element in posture and locomotion, the vertebral column holds critical information concerning the functional morphology and evolutionary development of positional behavior in primates. One parameter that is particularly informative is vertebral column length, especially in the lumbar region. The lumbar column is reduced (compared to closely related taxa) in several unrelated groups of primates, including hominoids, indrids,<sup>1</sup> and atelines

(Schultz, 1961; Erikson, 1963; Benton, 1967, 1974; Cartmill and Milton, 1977; Jungers, 1984; Shapiro, 1995). This reduction is brought about by decreased numbers of ver-

Contract grant sponsor: National Science Foundation; contract grant number BNS 8823083; Contract grant sponsor: University of Texas.

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Received 27 August 1996; accepted 23 November 1997.

tebrae, shortening of the vertebral bodies, or a combination of both (Benton, 1967; Schultz, 1961; Ankel, 1972; Shapiro, 1993; Ward, 1993; Sanders, 1995). Alternatively, the lumbar region may be unreduced in length, but relatively short in conjunction with an elongated thorax (e.g., in lorids;<sup>1</sup> Cartmill and Milton, 1977). The structure and orientation of lumbar articular processes (zygapophyses) limit lateral flexion and rotation, but permit movement in the ventrodorsal (sagittal) plane. Reduction in the length of the lumbar region thus decreases ventrodorsal bending moments about the intervertebral disks, and stiffens the lumbar region, while elongation of this region increases sagittal flexibility and range of motion (Nordin and Frankel, 1989; Ward, 1993; Sanders and Bodenbender, 1994; Sanders, 1995; Long et al., 1997).

Another important functional aspect of lumbar vertebrae is their main lever arms, the transverse and spinous processes. In general, perpendicularly or caudally oriented spinous processes and dorsolaterally oriented transverse processes are found in conjunction with shortened lumbar regions, and are associated with upright postures and/or movements that require "stiffening" of the lumbar region and the ability to resist ventral flexion (e.g., Benton, 1967; Ankel, 1972; Ward, 1993; Shapiro, 1993, 1995; Sanders and Bodenbender, 1994; Sanders, 1995). These features can be contrasted with those of primates that utilize more pronounced ventrodorsal flexion/extension movements of the spine in locomotion, especially during quadrupedal running and leaping from a pronograde position. Primates specializing in these behaviors usually have a relatively long lumbar region, with spinous processes pointing cranially, and transverse processes that are ventrally located and ventrocranially oriented (Benton, 1967; Ankel, 1972; Ward, 1993; Shapiro, 1993, 1995; Sanders and Bodenbender, 1994; Sanders, 1995).

Although comparative morphological data on primate vertebrae continue to accumulate, biomechanical explanations for vertebral diversity are often based on broad cat-

egories of locomotor and postural behaviors, rather than on the specific role of the spine during those behaviors. A more reliable way to test functional hypotheses about vertebral morphology is to directly examine the role of the spine during positional behavior, either in the field or the laboratory. While increasing attention is being paid to back function in the laboratory (Shapiro and Jungers, 1988, 1994; Nieschalk, 1991; Preuschoft et al., 1995; Shapiro and Demes, 1996) field studies rarely focus attention specifically on the mechanical demands placed on the spine (but see Hunt, 1991).

In this study, direct field observations of axial postures and movements are used to assess typical loads placed on the vertebral columns of four sympatric species of platyrrhine monkeys. Two species are atelines (*Ateles geoffroyi*, *Alouatta palliata*) and two are cebines (*Cebus capucinus*, and *Saimiri oerstedii*) (e.g. Schneider et al., 1996; see Ford and Davis, 1992, for alternative phylogenies). These observations are combined with a vertebral morphometric analysis on the same taxa (plus the other two ateline genera, *Brachyteles* and *Lagothrix*) in order to test functional hypotheses about primate vertebral morphology.

Atelines have figured prominently in primate postcranial functional research because of their morphological convergences with hominoids (e.g., Ashton and Oxnard, 1964; Erikson, 1963; Stern et al., 1977; Fleagle et al., 1981; Gebo, 1989; Rosenberger and Strier, 1989). In fact, atelines are especially important for studies of hominoid vertebral anatomy because they resemble some or all hominoids in several aspects of spinal morphology, including a reduced number of lumbar vertebrae compared to other primates (Schultz, 1961; Erikson, 1963; Benton, 1967), as well as the structure of their spinous and transverse processes (Erikson, 1963; Benton, 1967; Ankel, 1972). Thus atelines are a key group for understanding the function and evolution of the spine in nonhuman hominoids, and for providing insight into the evolution of upright posture and bipedalism in humans. The functional and evolutionary relevance of vertebral anatomy in atelines cannot be well understood, however, until morphological and be-

<sup>1</sup>Jenkins (1987) notes that Indridae and Loridae have priority over Indriidae and Lorisidae according to Article 29b(ii) of the International Code of Zoological Nomenclature. See Godfrey et al. (1995) for a more detailed discussion of this issue.

havioral variation within and between atelines and other platyrrhines is documented quantitatively.

While previous studies have quantified the positional behavior of atelines and cebines (Richard, 1970; Mendel, 1976; Mittermeier, 1978; Fleagle and Mittermeier, 1980; Schön Ybarra, 1984; Cant, 1986; Schön Ybarra and Schön, 1987; Fontaine, 1990; Boinski, 1989; Gebo, 1992), none has related systematic observations of back loading patterns during positional behaviors to platyrrhine vertebral anatomy. Moreover, the vertebral anatomy of these platyrrhines has been described qualitatively (Ankel, 1962, 1972; Benton, 1967), but quantitative analyses have been restricted to subsets of these taxa (Rose, 1975; Clauser, 1980; Ward, 1993) or have been confounded by the use of nonisometric variables for size standardization (e.g., trunk length or presacral length; Schultz, 1961). Currently, then, the literature provides only general discussions of vertebral function and little objective assessment of vertebral morphological or behavioral variation within this group.

The objectives of this study are to 1) quantify variation in vertebral morphology among and between atelines and cebines, 2) quantify and compare positional behavior in atelines and cebines with a particular focus on the loads placed on the spine during these behaviors, and 3) use these data to establish reliable links between lumbar form and function among these platyrrhines, and to evaluate hypotheses about vertebral form-function relationships in other primates.

## MATERIALS AND METHODS

### Behavior

**Study site and animals.** Field observations were conducted at Estacion Sirena, Parque Nacional Corcovado, Costa Rica. Data were collected during 37 non-consecutive days in July–August (mid wet season) 1994. The 1-km<sup>2</sup> study area contains various habitat types of maturing second growth and primary forest, including areas that were selectively cut prior to formation of the national park (L.E. Gilbert, pers. comm.). Structurally, the habitat offers a wide variety of support types, ranging from large trunks (>5 m) and branches to thin terminal

branches and tangled understory growth. Except in primary forest areas (where there are few branches below the high canopy), this habitat consists of branches with varied orientations (from oblique to horizontal) at most height levels.

The species observed in the study area are: *Ateles geoffroyi*, *Alouatta palliata*, *Cebus capucinus*, and *Saimiri oerstedii*. These taxa comprise a valuable sample for testing functional hypotheses because they vary in body size and are known to form somewhat of a behavioral continuum from most to least suspensory (Rosenberger and Strier, 1989), as described below.

*Ateles geoffroyi* is the largest of the four species; on average, males weigh 8.21 kg and females weigh 7.47 kg (Ford and Davis, 1992). Spider monkeys are primarily arboreal quadrupeds; however, they also show high frequencies of acrobatic suspensory locomotion (such as brachiation) as well as climbing (Richard, 1970; Mittermeier, 1978; Fleagle and Mittermeier, 1980; Cant, 1986; Fontaine, 1990). Their tails are also fully prehensile (Rosenberger, 1983; Lemelin, 1995) and used commonly in suspensory postures and locomotion (Richard, 1970; Mittermeier, 1978; Cant, 1986; Fontaine, 1990).

*Alouatta palliata* is a large primate, with body weights averaging 7.15 kg and 5.35 kg for males and females, respectively (Ford and Davis, 1992). Howler monkeys are primarily slow arboreal quadrupeds; they also climb frequently and occasionally bridge gaps in the canopy (Richard, 1970; Mendel, 1976; Fleagle and Mittermeier, 1980; Schön Ybarra, 1984; Cant, 1986; Schön Ybarra and Schön, 1987; Gebo, 1992). With the support of their fully prehensile tails (Rosenberger, 1983; Lemelin, 1995), howler monkeys also frequently employ suspensory postures (Mendel, 1976; Cant, 1986; Schön Ybarra, 1984; Schön Ybarra and Schön, 1987; Gebo, 1992).

*Cebus capucinus* is a small to mid-sized primate, with males and females averaging 3.87 kg and 2.67 kg, respectively (Ford and Davis, 1992). Like howlers and spider monkeys, capuchins are primarily arboreal quadrupeds (Fleagle and Mittermeier, 1980; Gebo, 1992). They also demonstrate frequent climbing activities, less frequent leaping, and

relatively rare bridging and suspensory postures (Fleagle and Mittermeier, 1980; Gebo, 1992) aided by their "semi-prehensile" tails (Rosenberger, 1983).

*Saimiri oerstedii* is the smallest primate in the research area; on average, females weigh 0.70 kg and males weigh 0.83 kg (Ford and Davis, 1992). When measurements are made outside of the breeding season, male average weight is approximately 0.75 kg (Boinski, 1989). *Saimiri* is an arboreal quadruped and frequent leaper that also climbs occasionally (Fleagle and Mittermeier, 1980; Boinski, 1989; Fontaine, 1990). Its tail is non-prehensile (Rosenberger, 1983), but may serve as a brace in tripod stances (Boinski, 1989).

**Data collection.** Data were obtained using scan sampling techniques<sup>2</sup> (Altmann, 1974). A total of 1,518 scan samples were collected (*Ateles*, N = 128; *Alouatta*, N = 185; *Cebus*, N = 1,004; *Saimiri*, N = 201). A focal animal was followed continuously for up to 10 minutes (range: 1–10 minutes), and its behavior was recorded at 1-minute intervals. If an animal was lost during the 10-minute sample, another animal in the group was selected at random for observation. A continuously operating timer controlled the

TABLE 1a. Behavioral categories recorded in scan samples

Category	Subcategory
Substrate orientation	Horizontal (0°–30°) Oblique (31°–60°) Vertical (61°–90°)
Posture relative to the substrate	Orthograde Semi-orthograde Pronograde
Tail use	Substantial support Partial support No support
Loading regime	Bending 1 Bending 2 Compression Tension Rest (no loading)

timing of the onset of each sample. In scan samples, the following information was recorded: 1) substrate orientation; 2) posture relative to the substrate; 3) positional behavior; 4) tail use; and 5) load acting on the vertebral column (see Tables 1a and 1b).

Tail use categories were based on the amount of body weight support provided by the tail. "Substantial support" was applied to cases where the tail was used as a principal or sole support for the animal, generally grasping overhead branches. In contrast, the "support" category pertained to behaviors in which the tail grasped or was wrapped around branches, but did not serve to hold up the body (e.g., when the tail was used to grasp the branch on which the animal was sitting or lying, or grasped overhead branches during quadrupedal walking). The "no support" category indicated that the tail was not being used as any form of weight support or brace.

The types of loads (bending 1, bending 2, compression, tension, and no load) were categorized based on the focal animal's posture relative to the substrate, the orientation of the substrate, and positional behavior (including tail use). The compression category was used for behaviors during which the craniocaudal length of the spine was oriented generally parallel to the line of gravity. Examples of these behaviors include sitting, bipedal standing, and vertical climbing and descent (both head-first and rear-first). Some behaviors were reclassified a posteriori into two qualitatively different categories: bending 1 and bending 2 (which

<sup>2</sup>Doran (1992) noted that instantaneous sampling may not adequately record brief events, ignores distances traveled, and may require large sample sizes. However, Doran (1992) found that scan sampling results do not vary significantly from those of locomotor bout sampling when bouts are weighted by distance traveled. To address the problem of sample size, we have included a comparison with results from previous studies on the positional behavior of these four genera (see Results).

Dagosto (1994) argued that both instantaneous and continuous sampling techniques may violate statistical assumptions of independence and random sampling. To avoid the former pitfall, runs tests were conducted on the 74 individual samples that ranged from 5 to 10 minutes each (there are no critical values for sequences less than 5 minutes; Sokal and Rohlf, 1981). Because these runs were evaluated based on data points being the same or different from previous points, it was assumed that any number of runs beyond the low critical number constituted a random sequence (i.e., random sequences included samples where the behavior changed every minute). Results from these tests indicated that the positional behaviors alternated significantly ( $P < .05$ ) in 51 of the 74 cases (i.e., there were at least enough runs in these samples to be considered random). Furthermore, the 1–4 minute samples represent 64% of the total data set, wherein independence is reasonably assured. The combination of these samples and the 51 random-sequence 5–10 minute samples includes over 87% of the total data set. Therefore, the 1-minute intervals were likely sufficient to record independent behavior events. If the non-random samples were not included in the analysis, potentially important information about the relative amount of time devoted to prolonged behaviors (e.g., "sit" or "lie") would be lost. In addition, every attempt was made to alternate between all members of the social group under observation; unfortunately, it was impossible to ensure random sampling due to the inability to recognize all individuals.



TABLE 1b. *Ethogram*<sup>1</sup>

Postural behaviors	Locomotor behaviors
Suspensory postures SUS: Suspensory posture. Suspension by any or all of the four limbs or tail.	Quadrupedal cursorial locomotion QRU: Quadrupedal running. QWA: Quadrupedal walking. TWA: Tripedal walking.
Nonsuspensory postures BST: Bipedal standing. INB: Inverted bipedalism. Standing bipedally on a support with the head oriented downward. The forelimbs are generally free. There is compression in the forelimbs, bending in the back, and tension in the prehensile tail (except in <i>Saimiri</i> ).	Locomotion Emphasizing the limbs in tension ASW: Arm-swinging. Bimanual suspensory locomotion with arm and trunk rotation. BRI: Bridging. Passage between gaps in the canopy that involves reaching with the forelimbs and grasping with the hindlimbs.
LIE: Lie. Laying on the back, side, or ventrum. QST: Quadrupedal standing. SIT: Sitting. Sitting in a hunched or orthograde posture.	Climbing activities QCL: Quadrupedal climbing. Quadrupedal, vertical ascent. QDH: Head-first quadrupedal descent. QDR: Rear-first quadrupedal descent.
TST: Tripedal standing. VCL: Vertical clinging. Grasping a vertical support in an orthograde posture.	Leaping and dropping BOD: Bounding descent. Asymmetrical head-first descent with forelimbs in compression and hindlimbs and back in tension. DRO: Dropping. Dropping from one support to another with minimal horizontal displacement. LEQ: Quadrupedal leaping. Leaping from a quadrupedal take-off position. LEV: Vertical leaping. Leaping from a vertical take-off position.

<sup>1</sup> List of all positional behavior codes and explanations used for analysis. Based on explanations from Fontaine (1990).

were not used in initial observations) based on the same criteria. The distinction between these two categories principally rests on whether the limbs and/or tail were used in overhead or under-body support. The classifications do not include the potential effects of soft tissues in redistributing the forces acting on the vertebrae (see below).

Bending 1 was assigned to behaviors which likely increased overall bending stress in the spine through overhead suspension. The activities in this category placed the back in a position that would entail relatively prolonged periods of ventrodorsal (sagittal plane) bending (e.g., bridging gaps in the canopy or suspensory hanging). In addition, the gravitational pull on the back was not diffused by support from the limbs on the substrate.

Bending 2 was applied to cases in which the positional behavior did not deviate greatly from a basic quadrupedal stance (including standing and walking quadrupedally). The use of the limbs as under-body rather than above-body support was assumed to decrease the amount of axial bending stress resulting from gravity. Hypothetically, the basic quadrupedal stance would

still result in some ventrodorsal bending loads on the spine. Epaxial and abdominal muscles may counter the tensile component of bending during quadrupedal standing, leaving net compression in the vertebral bodies (the "bow and string" arrangement; Slijper, 1946; Badoux, 1974). Yet even small muscular contractions may produce some ventrodorsal bending moments in the spine (Badoux, 1974). It is beyond the scope of the present study to quantify the contribution of soft tissues. Nevertheless, Badoux's (1974) observations justify the qualitative distinction made between bending 1 (during suspensory behaviors) and bending 2 (during quadrupedalism).

Leaping behaviors were also placed in the bending 2 category. Leaps included an initial burst of rapid extension during take-off, followed by flight and landing stages. Although relatively brief, take-off appears to involve bending stresses in the spine. In an analysis of the kinematics of horizontal leaping in vervet monkeys, Wells and Wood (1975) demonstrated that the force effects acting on the abdominal region in a downward direction generally increase until the

point of take-off, when the direction of the force shifts forward. These force vectors in combination with the placement of the limbs suggest that the spine sustains bending loads during take-off. In contrast, during flight, gravitational pull acts equally on the whole body; there are no loads placed disproportionately on the spine. During the impact of landing, the spine again may sustain bending stress for a brief period. However, it was assumed there would not be the same sustained axial bending during leaping as in suspensory bending behaviors.

The tensile loading category was applied to suspensory behaviors where substantial bending was unlikely. These behaviors consisted of suspension by one or both forelimbs without the overhead support of the tail. In addition, cases of suspension only by the tail (or the tail in conjunction with one or both hindlimbs) were classified as tension.

The loading category "rest" described cases where the spine would sustain negligible stresses. The only behavior included in this regime was "lie."

**Statistical analysis.** Chi-square contingency tables were used to test for significant differences in the frequencies of loading regimes, tail use, and positional behavior. Positional behavior was analyzed in three ways: as a combined sample of all positional behavior subcategories and with separate samples for postural and locomotor categories.

Follow-up tests were used to determine the source of variation found in contingency table analyses. One-group chi-square goodness-of-fit tests determined if there was significant variation from expected values (the mean frequency for all taxa) for the following: 1) each loading regime, 2) each posture relative to the substrate, 3) the two subcategories within postural behavior, 4) the four subcategories within locomotor behavior, and 5) the amounts of support during tail use.

**Comparison with previous studies.** The number of samples varied considerably among the subject species. Furthermore, the total number of samples for *Ateles*, *Alouatta*, and *Saimiri* was considerably lower than in

TABLE 2a. Sample sizes for morphological data (number of individuals)

Species	Transverse process orientation	All other variables
<i>Hylobates</i> spp. <sup>1</sup>	4	17
<i>Brachyteles arachnoides</i>	1	1
<i>Ateles paniscus</i>	4	5
<i>Ateles geoffroyi</i>	1	1
<i>Lagothrix lagothricha</i>	5	8
<i>Alouatta palliata</i>		3
<i>Alouatta seniculus</i>	5	12
<i>Cebus capucinus</i>		1
<i>Cebus apella</i>	4	16
<i>Cebus olivaceus</i>	2	
<i>Saimiri</i> spp. <sup>2</sup>	5	5

<sup>1</sup> Includes *H. lar*, *H. moloch*, *H. agilis*, *H. hoolock*, *H. muelleri*.

<sup>2</sup> Species unknown.

previous positional behavior studies. Therefore, it was necessary to ensure the utility and comparability of this smaller data set. In order to examine the potential for bias due to sampling error, the frequencies of behavioral subcategories (ranked) were compared to those obtained from other sources.

### Morphology

**Sample.** The morphological sample includes all four taxa observed in the field—*Ateles geoffroyi*, *Alouatta palliata*, *Cebus capucinus*, and *Saimiri oerstedii*. Morphological data for the remaining two ateline genera, *Brachyteles arachnoides* and *Lagothrix lagothricha*, and for one hominoid (*Hylobates*, mixed species; see Table 2a) were also included for comparative purposes. Due to rarity or unavailability of museum specimens, only very small samples of species matching those observed behaviorally could be obtained. Therefore, larger samples of congeneric species were also used for the morphological analysis (see Table 2a for sample sizes). Data for all species are reported, but morphological comparisons between behaviorally observed species and additional species revealed no significant differences (since data are adjusted for body size differences). Where appropriate for clarity, therefore, data for congeneric species were combined. Several lumbar vertebrae were measured for each specimen, but the results presented here focus on a representative midlumbar vertebra.

**Measurements.** All measurements were taken with digital calipers except transverse

TABLE 2b. Measurements of the diaphragmatic vertebra included in the calculation of the geometric mean

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Distance between the midpoints of the medial borders of the prezygapophyses
Distance between the midpoints of the lateral borders of the prezygapophyses
Width of the right prezygapophysis
Distance between the midpoints of the postzygapophyses
Width of the lamina
Thickness of the lamina
Midline ventrodorsal height of the cranial surface of the vertebral body
Maximum width of the cranial surface of the vertebral body
Midline ventrodorsal height of the caudal surface of the vertebral body
Maximum width of the caudal surface of the vertebral body
Length of the spinous process
Midline ventrodorsal height of the vertebral foramen
Maximum width of the vertebral foramen
Midline craniocaudal length of the ventral aspect of the vertebral body

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process orientation which was measured from photographic images using AutoCad software. Vertebrae were photographed in cranial view. To ensure precision and accuracy of measurements, the midline of each vertebra was aligned on a grid, and both vertebra and camera were leveled in two planes with a small carpenter's level. For the smallest vertebrae, an adjustable vertical rod with a flat end (attached perpendicularly to a horizontal framework) was used to orient the cranial surface parallel to the horizontal plane. Measurement error using this method is less than 5.0%.

Variations in the number of vertebrae and in vertebral body shape can have a significant impact on bending moments that occur about the intervertebral disks (Ward, 1993). Although bending moments may occur predominantly at the disks, the vertebral bodies themselves also appear to be subjected to bending moments (Gaudin and Biewener, 1992). Therefore, even in the absence of comparative measurements of the intervertebral disks, vertebral body shape serves as an accurate indicator of functional spinal variation among primates.

**Vertebral bodies.** The height, width, length, and cranial surface area of the lumbar vertebral bodies were measured in order to assess the relative length, flexibility, bending resis-

tance, and weight-bearing capabilities of the lumbar region.

1. Height: distance between the ventral and dorsal edges of the cranial surface of the vertebral body, measured in the median sagittal plane. Higher vertebrae are more resistant to bending in the sagittal plane.

2. Width: greatest distance across the cranial surface of the vertebral body in the coronal plane. Wider vertebrae are more resistant to bending in a horizontal plane, i.e. lateral bending.

3. Length: distance between the ventral edges of the cranial and caudal surfaces of the vertebral body, measured in the median sagittal plane. Reduction in the length of a vertebral body or the lumbar region as a whole decreases bending moments in any plane, and reduces overall flexibility (Ward, 1993).

4. Cranial surface area: estimate based on area of an ellipse,  $(h/2)(w/2)(\pi)$ , where  $h$  = height and  $w$  = width. Resistance to compressive or tensile forces, and overall weight-bearing capability of the vertebra increases with vertebral body surface area.

**Transverse processes.** The angular orientation of the transverse processes in a ventrodorsal plane was measured in order to assess the leverage of flexor and extensor muscles in the lumbar region. The angle measured was that formed by 1) a line connecting the base with the tip of the transverse process, and 2) a line parallel to a median sagittal plane through the vertebra. A value of 90° indicates processes that are oriented perpendicularly to the sagittal plane, values less than 90° indicate ventrally oriented processes, and values greater than 90° indicate dorsally oriented processes.

**Spinous processes.** Previous research has demonstrated that significant differences among atelines and *Cebus* in the dorsal projection of lumbar spinous processes are inconsistent and exhibit little functional pattern among species (Shapiro, 1991). Dorsal projection is not considered further here, but preliminary observations on the orientation of spinous processes are described qualitatively.

TABLE 3. Frequency of back loading regimens

Taxon	Compression	Bending 1	Bending 2	Rest	Tension
<i>Ateles</i>	52.3%	18.8%	7.8%	6.3%	14.8%
<i>Alouatta</i>	53.0%	8.1%	20.0%	14.6%	4.3%
<i>Cebus</i>	52.4%	4.8%	28.8%	11.9%	2.2%
<i>Saimiri</i>	41.8%	3.0%	51.2%	4.0%	0.0%

**Body size.** In order to compare linear dimensions of vertebrae among taxa that vary in body size, each raw measurement was divided by the geometric mean of 14 measurements taken on the diaphragmatic vertebra in each individual (See Table 2b and Mosimann and James, 1979; Jungers et al., 1995). The diaphragmatic vertebra (with thoracic-like prezygapophyses and lumbar-like postzygapophyses) was chosen because it is morphologically and functionally comparable across taxa and readily identifiable (Washburn and Buettner-Janusch, 1952; Erikson, 1963; Shapiro, 1993). Rather than using species estimates of body weight for size-adjustment, the geometric mean was used as a body size "surrogate" because it is specific to each individual museum specimen. Use of the geometric mean minimizes the noise associated with using species estimates of body weight with small sample sizes. In addition, Jungers et al. (1995) recently demonstrated that this approach successfully "swept away" isometric size when tested on an (artificially) isometrically scaled sample. Species means of the geometric mean and species estimates for body weights are very highly correlated ( $r = .98$ ), further justifying the use of the geometric mean as a size substitute.

**Statistical analysis.** ANOVA in conjunction with unplanned comparisons among means were used to test for interspecific differences among size-adjusted variables. Pairwise comparisons were carried out using the GT2 test. The GT2 test employs conservative experimentwise error rates and is recommended when sample sizes are very unequal (Sokal and Rohlf, 1981). If variances were heteroscedastic, the Games and Howell method was used for pairwise comparisons (used for relative region length only; see Results). Variables were regressed on the geometric mean in logarithmic space (natural logs) in order to examine more

closely the effects of body size on vertebral morphology. Since these represent Model II regressions and were not used for predictive purposes, the line fitting technique employed was reduced major axis (Sokal and Rohlf, 1981; Jungers, 1985; Aiello, 1992).

## RESULTS

### Behavior

**Back loading regimens.** The four main study taxa differed significantly in the frequency of overall loading patterns ( $P < .0001$ ) (Table 3). In follow-up tests, there was variation in the frequency of bending 1 ( $P < .0005$ ) (Table 3, Fig. 1). Atelines clearly sustained bending 1 (through suspensory activities) more often. Within this group, *Ateles* had more than twice the frequency of bending 1 than did *Alouatta*. Among cebines, *Cebus* was subjected to a higher frequency of bending 1 than was *Saimiri*. Tensile loading also varied across taxa ( $P < .0001$ ), following the same pattern as bending 1 (with *Ateles* having the highest frequency and *Saimiri* the lowest) (Fig. 1). Bending 2 differed substantially among the four species ( $P < .0001$ ). However, the trend in frequencies was reversed, with the highest frequency in *Saimiri* and the lowest in *Ateles* (Table 3, Fig. 2). The frequency varied significantly in cases when no back loading was apparent ( $P < .05$ ). This loading regime did not follow either of the previous patterns; rest was most common in *Alouatta*, followed by *Cebus*, *Ateles*, and *Saimiri*. In contrast, there were no significant differences in the frequencies of compression across taxa (Table 3).

**Posture relative to the substrate.** The four species varied significantly in the overall use of postures ( $P < .0001$ ) (Table 4, Figs. 1, 2). In follow-up tests, significant differences were found for orthogrady ( $P < .0001$ ). *Ateles* was clearly orthograde most often,



followed by *Alouatta*, *Cebus*, and *Saimiri* (Fig. 1). Pronogrady also varied substantially ( $P < .0001$ ), following the opposite trend among the subject species—*Saimiri* was the most pronograde while *Ateles* was the least (Fig. 2). The four species did not differ significantly with respect to the frequency of semi-orthograde postures.

**Positional behavior.** Overall positional behavior frequencies varied significantly across taxa ( $P < .0001$ ). There were also significant differences across taxa within each of the subcategories of positional behavior, posture and locomotion ( $P < .0001$ ).

**Posture.** Resembling the trends for bending 1, tension, and orthograde, atelines (particularly *Ateles*) more frequently engaged in suspensory postures than cebines (*Saimiri* again having the lowest frequency) ( $P < .0001$ ; Table 5; Fig. 1). However, the frequency of nonsuspensory postures did not vary significantly among the four species.

**Locomotion.** The atelines engaged more frequently than either cebine in suspensory-

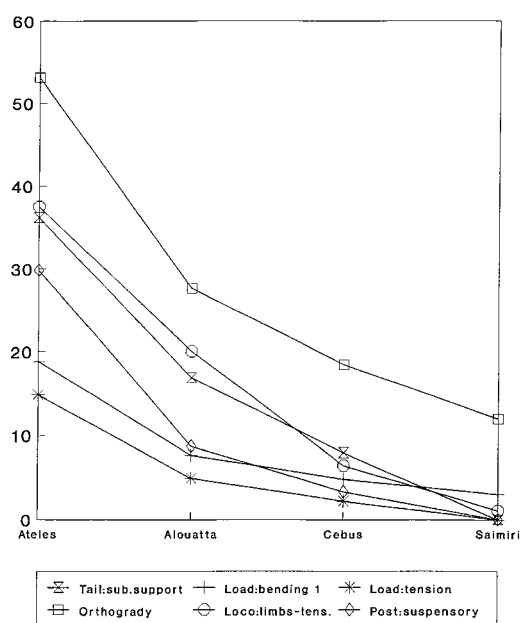


Fig. 1. Behaviors that differ significantly among the sample taxa and follow an increasing trend in frequency from *Saimiri* to *Cebus* to *Alouatta* to *Ateles*. See Tables 3–7 for behavior categories.

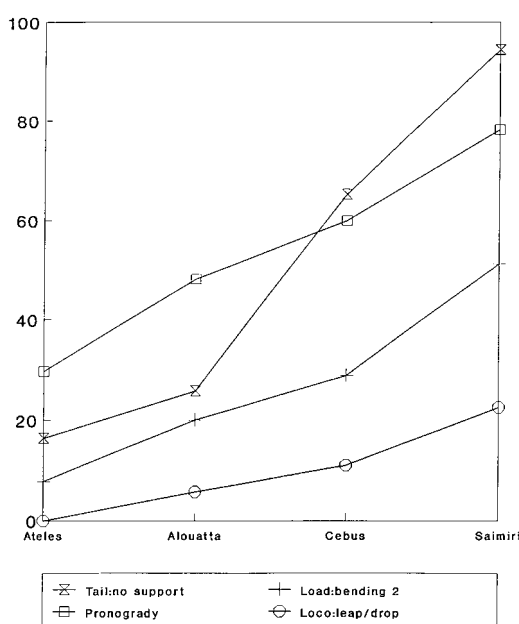


Fig. 2. Behaviors that differ significantly among the sample taxa and follow an increasing trend in frequency from *Ateles* to *Alouatta* to *Cebus* to *Saimiri*. See Tables 3–7 for behavior categories.

type locomotor behaviors in which the limbs are used in tension (e.g. arm-swinging, bridging) ( $P < .0001$ , Table 6; Fig. 1), with decreasing frequencies forming a continuum from *Ateles* to *Alouatta* to *Cebus* to *Saimiri*. Leaping and dropping frequencies varied substantially ( $P < .0001$ ). The leaping and dropping frequencies increase from *Ateles* to *Saimiri* in a trend opposite to that found for suspensory locomotion, and similar to the trends exhibited by bending 2 and pronogrady (Fig. 2). Frequencies of quadrupedal cursorial locomotion also differed among species ( $P < .05$ ). However, there was no consistent pattern for the two subfamilies. *Cebus* and *Alouatta* locomoted quadrupedally most often, followed by *Saimiri* and *Ateles*. How-

TABLE 4. The frequency of postures relative to the substrate

Taxon	Orthograde	Semi-orthograde	Pronograde
<i>Ateles</i>	53.1%	17.2%	29.7%
<i>Alouatta</i>	27.6%	24.3%	48.1%
<i>Cebus</i>	18.4%	21.7%	59.9%
<i>Saimiri</i>	11.9%	10.0%	78.1%

TABLE 5. Frequency of postural behaviors<sup>1</sup>

Taxon	Suspensory postures	Nonsuspensory postures
<i>Ateles</i>	29.8%	70.2%
<i>Alouatta</i>	8.7%	91.3%
<i>Cebus</i>	3.3%	96.7%
<i>Saimiri</i>	0.0%	100.0%

<sup>1</sup> Each subcategory's relative contribution to the total number of postural behaviors.

ever, despite significant variation in frequencies, quadrupedalism represented the most common form of locomotion for all four species (although suspensory locomotion was equally common in *Ateles*) (Table 6). Finally, no significant differences were found in the frequency of climbing behaviors.

**Tail use.** Significant variation was found in overall tail use frequencies across species as well as within each tail use category ( $P < .0001$ ; Table 7). *Ateles* demonstrated the highest frequency for the use of the tail as a substantial (primary) support for body weight, concomitant with its frequent use of suspensory postures and locomotion. *Alouatta*, which also has a fully prehensile tail, was second in this tail use category, followed by *Cebus* (with a "semi-prehensile" tail) and *Saimiri* (which exhibited no strong grasping abilities) (Fig. 1). However, *Alouatta* was first among the four species in the frequency of the tail as a partial support; *Ateles* was second in this category, *Cebus* third, and *Saimiri* fourth (Table 7). As would be expected from these results, *Saimiri* exhibited the highest frequency for behaviors lacking any support from the tail, followed by *Cebus*, *Alouatta*, and *Ateles* (Fig. 2).

As noted, *Saimiri* was conspicuous in lacking prehensility in its tail. Therefore, it was important to determine if *Saimiri*'s inclu-

TABLE 7. Frequency of tail use as a weight-bearing support

Taxon	Substantial support	Support	No support
<i>Ateles</i>	36.2%	47.4%	16.4%
<i>Alouatta</i>	16.8%	57.4%	25.8%
<i>Cebus</i>	7.9%	26.9%	65.2%
<i>Saimiri</i>	0.0%	5.6%	94.4%

sion in the sample was clouding any similarity between the other three species. However, when *Saimiri* was excluded from the tests, significant differences remained in all three categories.

**Comparison with previous studies.** To examine the potential effects of sampling error in the present study, we include a comparison with previous research. The relative frequency of positional behaviors and the ranks according to frequency are listed in Table 8. Despite the small samples for *Ateles*, *Alouatta*, and *Saimiri*, the ranking of positional behavior frequencies in this study was virtually identical to the mean ranked orders from prior studies. The only reversal in rank occurred in *Alouatta*. In contrast to the present study, most authors have recorded a higher frequency for climbing than for locomoting with the limbs in tension (e.g., bridging) in this species. However, there are broad ranges in the reported frequencies for both climbing (0.0%–57.1%) and suspensory locomotion (0.0%–34.4%). The present results fall within these ranges (11.4% and 20.0%, respectively). Apart from ranking order, there are some discrepancies in the mean frequencies from previous work and the present results—most notably, the 20.2% for climbing in *Saimiri* from this study vs. the 3.8% mean from elsewhere. Unfortunately, it is difficult to determine if these differences are due solely to sampling bias. They may be related to other factors such as species and habitat differences (only Boinski, 1989, studied *S. oerstedi*) or dissimilar behavior definitions.

### Morphology

**Lumbar region length.** The length of the lumbar region of the vertebral column is a function of the number of lumbar vertebrae as well as the craniocaudal length of indi-

TABLE 6. Frequency of locomotor behaviors<sup>1</sup>

Taxon	Quadrupedal cursorial locomotion	Locomotion emphasizing the limbs in tension	Climbing activities	Leaping/dropping
<i>Ateles</i>	37.5%	37.5%	25.0%	0.0%
<i>Alouatta</i>	62.9%	20.0%	11.4%	5.7%
<i>Cebus</i>	63.7%	6.4%	19.0%	10.9%
<i>Saimiri</i>	56.2%	1.1%	20.2%	22.5%

<sup>1</sup> Each locomotor behavior subcategory's relative contribution to the total number of locomotor behaviors.

TABLE 8. Positional behavior: Comparison with previous studies<sup>1</sup>

Genus	Source	Behavior ranking and frequency						
		Postural behaviors		Locomotor behaviors				
		Suspensory postures	Nonsuspensory postures	Quadrupedal cursorial locomotion	Locomotion with limbs in tension	Climbing activities	Bipedalism	Leaping and dropping
<i>Ateles</i>	Present study	2 (29.8%)	1 (70.2%)	1 (37.5%)	1 (37.5%)	3 (25.0%)	4 (0.0%)	4 (0.0%)
	Previous studies mean	2 (33.2%)	1 (66.8%)	2 (38.0%)	1 (40.3%)	3 (19.9%)	5 (1.4%)	4 (5.1%)
<i>Alouatta</i>	Present study	2 (8.7%)	1 (91.3%)	1 (62.9%)	2 (20.0%)	3 (11.4%)	5 (0.0%)	4 (5.7%)
	Previous studies mean	2 (11.2%)	1 (88.5%)	1 (59.3%)	3 (8.4%)	2 (25.8%)	5 (0.0%)	4 (4.6%)
<i>Cebus</i>	Present study	2 (3.3%)	1 (96.7%)	1 (63.7%)	4 (6.4%)	2 (19.0%)	5 (0.0%)	3 (10.9%)
	Previous studies mean	2 (6%)	1 (94%)	1 (70.0%)	4 (2.0%)	2 (16.3%)	5 (0.5%)	3 (11.0%)
<i>Saimiri</i>	Present study	2 (0.0%)	1 (100.0%)	1 (56.2%)	4 (1.1%)	3 (20.2%)	5 (0.0%)	2 (22.5%)
	Previous studies mean	2 (1.5%)	1 (98.6%)	1 (77.6%)	4 (0.4%)	3 (3.8%)	5 (0.2%)	2 (17.7%)

<sup>1</sup> Behavioral results from the present and previous studies are ranked according to relative frequency among postural and locomotor behaviors. Also included are the frequency of behaviors within categories (i.e., "Postural" and "Locomotor"). To directly compare the results from several studies, it was necessary to group behaviors into the subcategories used in the present analysis (which may vary from original published results). In addition, where behaviors had been reported in several specific contexts (e.g., "Travel," "Feeding," and "Foraging"), the contexts were combined to give an average frequency for each behavioral subcategory. Despite the general similarity across studies, non-standard behavior definitions are likely responsible for some of the disparity in frequencies. Species and habitat differences (including the effects of seasonality) may also contribute to the variation in results (Mittermeier, 1978; Gebo and Chapman, 1995a, 1995b).

The previous mean was obtained from published studies. Sources for *Ateles* include: Richard (1970), Mittermeier (1978), Fleagle and Mittermeier (1980), Cant (1986), and Fontaine (1990). Sources for *Alouatta* include: Richard (1970), Mendel (1976), Fleagle and Mittermeier (1980), Schön Ybarra (1984), Schön Ybarra and Schön (1987), Cant (1986), Gebo (1992). Sources for *Cebus* include: Fleagle and Mittermeier (1980) and Gebo (1992). Sources for *Saimiri* include: Fleagle and Mittermeier (1980), Boinski (1989), and Fontaine (1990).

vidual vertebral bodies (and intervertebral disks which cannot be measured in dried skeletal specimens). The average number of lumbar vertebrae<sup>3</sup> for each platyrrhine taxon is listed in Table 9, including a comparison to *Hylobates*. The numbers follow somewhat of a continuum, with *Hylobates*/*Ateles*/*Brachyteles* and *Saimiri* the most divergent. On average, atelines have fewer lumbar vertebrae than either *Cebus* or *Saimiri*. Similarly, *Ateles* and *Brachyteles* have the relatively shortest vertebral bodies (which are statistically indistinguishable from those of *Hylobates*), and *Saimiri* has the longest ( $P \leq .05$ ). The remaining three taxa have similar values, with *Lagothrix* exhibiting a slight reduction (Fig. 3).

Vertebral number and relative vertebral body length were also combined to give a rough estimate of the relative length of the

lumbar region as a whole. *Ateles* and *Brachyteles*, with both the fewest number of lumbar vertebrae and the relatively shortest vertebral bodies, have the relatively shortest region lengths, and their region lengths are convergent with that of *Hylobates* (Fig. 4). These results contrast with those of Benton (1967), who attributed reduction in ateline lumbar regions to reduction in numbers of vertebrae only, and are not easily comparable with those of Schultz (1961). Schultz (1961) standardized relative vertebral body length by trunk length or length of the presacral vertebral column, both of which are likely to be nonisometric (e.g., Jungers, 1984). *Saimiri*, with the most numerous and longest lumbar vertebrae, has the relatively

TABLE 9. Number of lumbar vertebrae (zygapophyseal definition)

Taxon	Mean	Range	N
<i>Hylobates</i>	5.4	5–6	21
<i>Brachyteles</i>	6.0	—	1
<i>Ateles</i>	5.6	5–6	6
<i>Lagothrix</i>	6.9	6–8	11
<i>Alouatta</i>	7.5	5–8	17
<i>Cebus</i>	8.1	7–9	17
<i>Saimiri</i>	9.0	—	5

<sup>3</sup>Lumbar vertebrae were defined by zygapophyseal shape and orientation, rather than by lack of ribs. By this definition, lumbar vertebrae are those with prezygapophyses that are concave and have dorsomedially oriented articular surfaces. The postzygapophyses are convex with ventrolaterally oriented articular surfaces. This definition is considered to be more functionally relevant for understanding the lumbar region, because it reflects the types of movements (i.e. sagittal flexion/extension) permitted at the joints (Washburn and Buettner-Janusch, 1952; Washburn, 1963; Erikson, 1963; Shapiro, 1993).

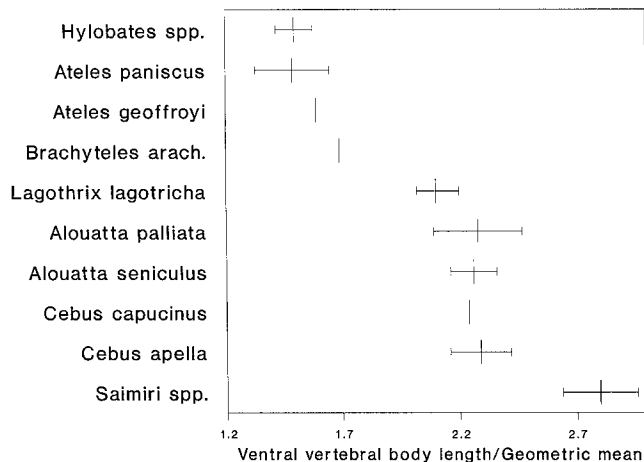


Fig. 3. Means  $\pm 1$  standard deviation of the ventral length of a midlumbar vertebral body divided by the geometric mean of 14 variables measured on the diaphragmatic vertebra. For *Brachyteles* and *Ateles* the midlumbar vertebra is L3, for the other taxa, L5. Divergence in values between a) *Hylobates/Brachyteles/Ateles*, b) *Alouatta/Cebus*, and c) *Saimiri* is significant at  $P \leq .05$ . *Lagothrix*'s vertebral body is intermediate in length—it is significantly longer than those of *Hylobates/Brachyteles/Ateles*, and significantly shorter than those of *Cebus* and *Saimiri* ( $P \leq .05$ ). *Lagothrix*'s vertebral body is also shorter than that of *Alouatta*, but not significantly so. Lack of statistical significance between *Lagothrix* and *Alouatta* is likely to be an artifact of small sample sizes or large variances because *Lagothrix* and *Cebus* differ significantly, and *Alouatta* and *Cebus* have similar values.

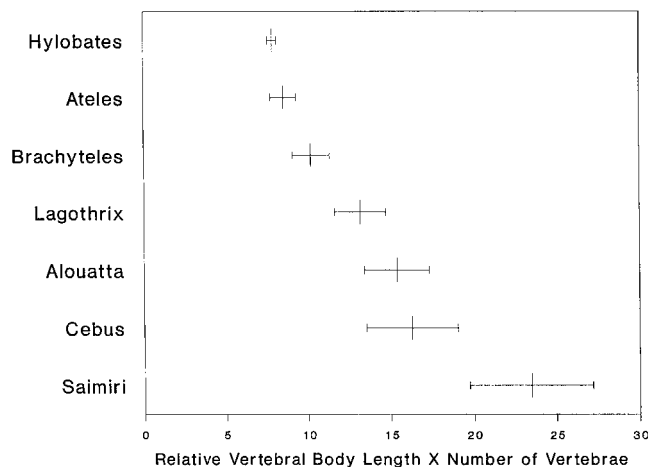
longest lumbar region length, while *Alouatta* and *Cebus* are indistinguishable in lumbar region length. Due to fewer vertebrae and a slight reduction in vertebral body length, region length in *Lagothrix* is intermediate between *Hylobates/Ateles/Brachyteles* and *Alouatta/Cebus*, but does not differ significantly from either group.

**Vertebral body length: Relationship to body size.** Relative lengths of the vertebral bodies among these taxa are not highly correlated with differences in body size ( $r = 0.71$ ), which is evident in the similarity of values between *Alouatta* and the much smaller sized *Cebus* (Fig. 3). The RMA regression line of vertebral body length on the

geometric mean is negatively allometric (slope = 0.59), but the 95% confidence intervals of the slope include the predicted isometric slope of 1.0. However, the wide scatter of points about the regression line (Fig. 5) suggests that morphological differences among the taxa are due to behavioral/functional variation, rather than size alone. For example, *Ateles* has relatively short vertebral bodies for its size, while *Alouatta* has longer vertebral bodies than expected for its size (thus resembling the smaller sized *Cebus*).

**Vertebral body width and height.** Vertebral body width (not figured) is well correlated with ( $r = 0.95$ ) body size among the six

Fig. 4. Relative length of the lumbar region. This is not a "true" length, but was estimated for each species by calculating  $L \cdot N$ , where  $L$  = the mean of relative vertebral body length values (see Fig. 1) for all lumbar vertebrae measured for that species and  $N$  = the mean number of vertebrae for the species. Divergence in values between a) *Hylobates/Brachyteles/Ateles*, b) *Alouatta/Cebus*, and c) *Saimiri* is significant at  $P \leq .05$ . *Lagothrix*'s lumbar region is significantly shorter than that of *Saimiri* ( $P \leq .05$ ) and is intermediate between *Hylobates/Brachyteles/Ateles* and *Alouatta/Cebus* but does not differ significantly from either of these two groups.





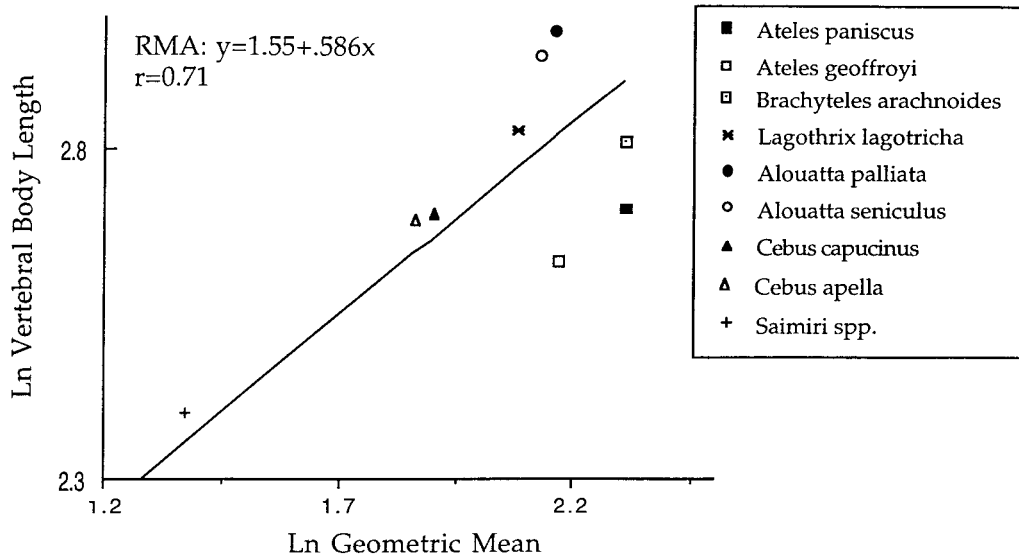


Fig. 5. RMA regression of vertebral body length on the geometric mean of the diaphragmatic vertebra (natural logs of species means).

platyrrhines. The slope is negatively allometric ( $b = 0.83$ ), but the 95% confidence intervals include isometry. Isometric scaling indicates that the larger species do not have relatively wider or narrower vertebrae than the smaller species. Comparisons among means were somewhat suggestive of a trend for the larger atelines to have relatively narrower vertebrae than the smaller cebines (i.e., negative allometry), but significant differences were inconsistent. Therefore we would conservatively conclude (based on these relatively small sample sizes) that vertebral body width does not appear to be a useful indicator of either behavioral or size-related differences among these platyrrhines.

In contrast to vertebral body width, the ventrodorsal height of the vertebral body is well correlated with body size and scales positively allometrically (Fig. 6). In other words, larger platyrrhines (as well as *Hylobates*) have relatively higher (i.e. ventrodorsally deeper) vertebrae than the smaller taxa. More specifically, comparisons among means (Fig. 7) indicate that atelines as a group have significantly higher vertebrae than either *Cebus* or *Saimiri*, and *Cebus* has significantly higher vertebrae than *Saimiri*.

There are no differences within the atelines.<sup>4</sup> Since resistance to bending is proportional to height squared (Slipper, 1946), it is reasonable to infer that differences in height are related to the larger bending forces associated with the larger body sizes of the atelines. However, because the taxa included in the regression differ by size *as well as* behaviorally, allometric shape differences cannot necessarily be attributed to size alone. The larger platyrrhines might also have relatively higher vertebrae in order to resist the increased bending stresses brought about by the behaviors they choose or are limited to *because* of their body size (Fleagle, 1985), as discussed below.

**Area of the cranial surface of the vertebral body.** Among these taxa, the area of the cranial surface of the lumbar vertebral bodies (a function of width and height) is well correlated with body size and scales isometrically (not figured). In other words, the sample taxa do not differ in vertebral

<sup>4</sup>Separate regressions run on individual data points rather than species means indicate positive allometry of vertebral body height for all taxa (consistent with Figure 6), positive allometry within cebines, and isometry within atelines (both consistent with Figure 7).

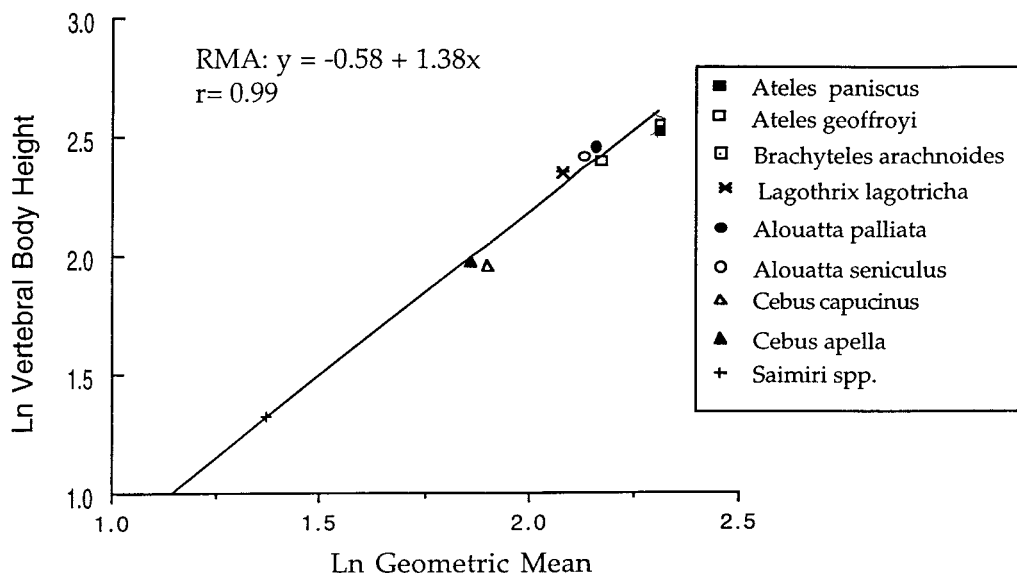


Fig. 6. RMA regression of vertebral body height (i.e. ventrodorsal diameter of the cranial surface) on the geometric mean of the diaphragmatic vertebra (natural logs of species means).

body surface area relative to body size, and therefore this dimension is not useful as an indicator of behavioral or size-related differences.

**Transverse process orientation.** Previous qualitative descriptions of transverse process variation among primates have brought attention to the distinction between atelines and other monkeys. That is, atelines (like gibbons) are known to have transverse processes that are oriented approximately perpendicular to the sagittal plane (Ankel,

1962, 1972; Benton, 1967) while other monkeys are usually categorized as having more ventrally oriented processes. The quantification of this parameter confirms the distinction between atelines and *Cebus/Saimiri*—the ateline values lie at or near 90° and are significantly higher in value than those of either *Cebus* or *Saimiri* (Fig. 8). Quantification also reveals that *Saimiri* has more ventrally oriented transverse processes than does *Cebus* (their values, though clearly divergent, are not statistically significant).

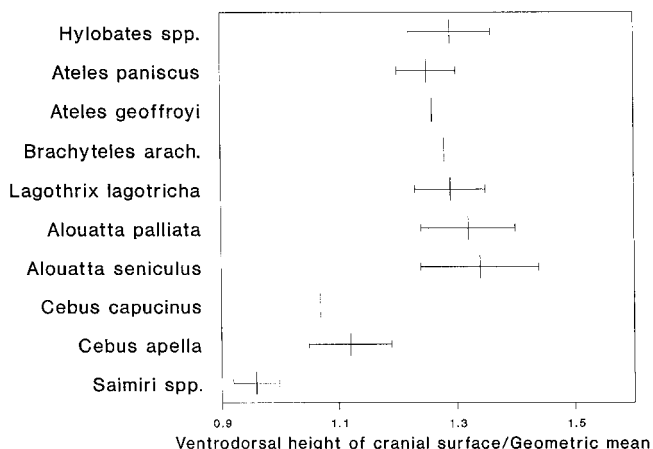
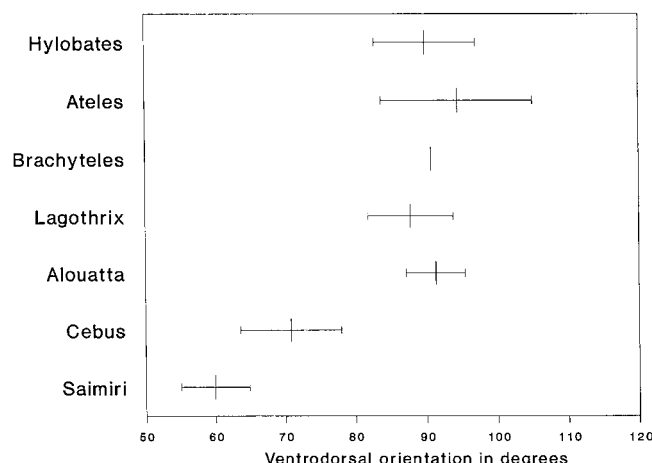


Fig. 7. Means  $\pm 1$  standard deviation of ventrodorsal height measured on the cranial surface of a midlumbar vertebral body, divided by the geometric mean of 14 variables measured on the diaphragmatic vertebra. For *Hylobates*, *Brachyteles* and *Ateles* the midlumbar vertebra is L3, for other taxa, L5. Gibbons and atelines as a group have significantly higher vertebrae than those of *Cebus* and *Saimiri*, and *Cebus* has significantly higher vertebrae than does *Saimiri* ( $P \leq .05$ ).

Fig. 8. Means  $\pm 1$  standard deviation of the ventrodorsal orientation (in degrees) of the transverse processes of a midlumbar vertebra. Values represent average of right and left sides. Ninety degrees indicates an orientation perpendicular to a sagittal plane through the vertebra; smaller values indicate more ventrally oriented transverse processes. Gibbons and atelines have approximately perpendicularly oriented transverse processes which differ significantly from the values for *Cebus* and *Saimiri* ( $P \leq .05$ ). *Saimiri* has more ventrally oriented transverse processes than does *Cebus*, but the difference is not statistically significant.



The distinction between *Cebus* and *Saimiri* has not been noted previously (qualitatively or quantitatively) and is important given the behavioral differences between them (see below).

#### Summary of morphological results.

*Atelines vs. cebines.* 1) All atelines have relatively higher (i.e. ventrodorsally deeper) lumbar vertebral bodies than cebines. Vertebral body height in atelines is convergent with that of *Hylobates*. 2) All atelines have perpendicularly oriented lumbar transverse processes, in contrast to the more ventrally oriented transverse processes of cebines. Transverse process orientation in atelines is convergent with that of *Hylobates*.

*Among atelines.* 1) *Brachyteles* and *Ateles* have relatively shorter lumbar vertebral bodies and lumbar regions than the other atelines, converging with *Hylobates*. The lumbar region of *Lagothrix* is slightly more reduced than that of *Alouatta*. Compared to other atelines, *Alouatta* has relatively long vertebral bodies and a relatively long lumbar region, resembling *Cebus* in these parameters.

*Among cebines.* 1) *Cebus* has higher (i.e. ventrodorsally deeper) lumbar vertebral bodies than does *Saimiri*. 2) *Saimiri* has longer lumbar vertebral bodies and a relatively longer lumbar region than does *Cebus*. 3) *Saimiri* has more ventrally oriented lumbar transverse processes than does *Cebus* (the

difference approaches, but does not reach, statistical significance).

#### DISCUSSION AND CONCLUSIONS

The lumbar morphology of atelines as a group is distinct from that of the cebines, but there are also clear differences in lumbar morphology within both of these groups. Most importantly, quantitative behavioral data indicate that the mechanical demands to which the spine is subjected during posture and locomotion are well reflected in the lumbar vertebral structure of these platyrrhines. Lumbar form-function relationships in *Ateles*, *Alouatta*, *Cebus*, and *Saimiri* are summarized below. We are also able to comment on vertebral structure and function in *Brachyteles* and *Lagothrix*, the two atelines for which much less information on behavior is available. Finally, these data are used to evaluate hypotheses regarding the function and evolution of lumbar reduction in primates.

##### Atelines vs. cebines

In contrast to cebines, atelines share an approximately perpendicular orientation of the transverse processes (confirming previous qualitative descriptions) and ventrodorsally elongated vertebral bodies. These same features are convergent in atelines and gibbons, as are many other aspects of their postcrania (Erikson, 1963; Ashton and Oxnard, 1964; Rosenberger and Strier, 1989). The orientation (perpendicular to a sagittal

plane) and placement of the transverse processes (i.e. at or near the body/pedicle junction) (Mivart, 1865; Benton, 1967; Ankel, 1962, 1972; Filler, 1986; Kelley, 1986; Shapiro, 1993) are likely associated with overall torso shape (e.g., Ward, 1993) and also indicate that the epaxial muscles attached to them lie near or just behind the axis of extension located in the intervertebral disk. Therefore, in atelines and gibbons the back muscles are well placed for resisting ventral flexion (i.e. stabilizing the lumbar region against bending in the ventrodorsal plane) and for recovering the spine from a flexed position, but not for hyperextension. This morphological adaptation is consistent with the behavioral data for *Ateles*, given its high frequencies of behaviors that induce bending stress on the spine. The reason for *Alouatta's* resemblance to the other atelines in transverse process morphology is less obvious, but these features may be an adaptation in *Alouatta* to resist bending during bridging or perhaps for more deliberate quadrupedalism (Rosenberger and Strier, 1989). Alternatively, *Alouatta's* transverse processes may reflect a primitive retention from a more suspensory evolutionary history (e.g., Kelley, 1986; Hartwig and Cartelle, 1996).

Vertebral body height is positively allometric among all sample taxa (but not within atelines), driven by the increase in size of atelines as a group compared to *Cebus* and *Saimiri*. Positive allometry may be interpreted to mean that body size alone is responsible for the relatively higher vertebral bodies characterizing atelines. However, since atelines are distinct behaviorally from the cebines, the influences of body size and behavior cannot be separated. In other words, atelines do not necessarily have relatively higher vertebrae in order to maintain functional equivalence with the smaller cebines. Rather, the behaviors preferred by atelines because of their larger body size (i.e. more suspensory, below-branch, or relatively more cautious behaviors) differ from those of cebines. These behavioral differences are likely to influence the vertebral anatomy of these platyrrhines. Ventrodorsal elongation of the vertebral bodies provides resistance to bending in the sagittal plane. Therefore, like that of transverse process

orientation, the distribution of values for vertebral body height are generally consistent with the fact that *Ateles* and *Alouatta* have higher frequencies of bending 1 than either of the cebines (albeit in this behavior, *Ateles* has a higher frequency than *Alouatta*; see below).

### Atelines

The atelines are known to form somewhat of a continuum with respect to both positional behavior and postcranial anatomy (Erikson, 1963; Rosenberger and Strier, 1989). This appears to hold true for vertebral form and function, as described below.

### Ateles/Brachyteles

Despite the similarity of all atelines in transverse process morphology and vertebral body height, there are distinct morphological differences among them. *Ateles* and *Brachyteles* have the relatively shortest lumbar vertebral bodies and lumbar region lengths, both resembling *Hylobates* in this respect. Because shortening the lumbar region theoretically minimizes bending moments, this finding corresponds well with the behavioral results—*Ateles* has the highest frequencies of behaviors that subject the vertebral column to potentially high bending loads (i.e., bending 1). That is, *Ateles'* frequent use of the prehensile tail as a substantial support during suspensory postures and locomotor behaviors such as arm-swinging can be presumed to load the spine in bending.

*Ateles* has the highest frequency of orthograde posture, which is often thought of in conjunction with compressive loading of the spine. However, orthograde in *Ateles* occurred most frequently during the types of suspensory activities that load the spine in tension or bending (e.g., bimanual suspension or suspension by forelimbs and tail, respectively), not axial compression. Therefore, given the relative infrequency of compressive orthograde in *Ateles*, it is not surprising that its intervertebral surface areas are not enlarged compared to the other sample taxa (since enlargement of this parameter would minimize compressive loads). In fact, predicted compressive loading did not differ significantly in frequency among



any of the taxa observed behaviorally. *Ateles* also engages in the highest frequency of tension-producing behaviors. Since tension would likewise be resisted by enlargement of intervertebral surface area (Swartz, 1993), we must conclude that we found no direct evidence of vertebral adaptation to tension in *Ateles*. More likely, resistance to tension is provided by muscle activity, which was not assessed here.

*Brachyteles* resembles *Ateles* morphologically in having a shorter lumbar region and shorter vertebral bodies in comparison to the other taxa. Much less is known about the positional behavior of *Brachyteles* than that of *Ateles*. However, like *Ateles*, *Brachyteles* appears to engage in relatively high frequencies of suspensory postures and locomotor behaviors in which the tail is used often in substantial support (Nishimura et al., 1988; Young et al., 1983 as summarized in Nishimura et al., 1988; Rosenberger and Strier, 1989). These types of behaviors are associated with bending stress on the spine and would therefore be well resisted by lumbar structure in *Brachyteles*.

Finally, preliminary observations indicate that *Ateles* and *Brachyteles* are similar in lumbar spinous process shape and orientation (see also Ankel, 1962, and Erikson, 1963, for illustrations and descriptions). Their square-tipped, approximately perpendicularly oriented spinous processes resemble those of hominoids, indrids, and lorids, suggesting an adaptation to suspensory, or generally "antipronograde" postures and locomotor behaviors (Mivart, 1865; Straus and Wislocki, 1932; Ankel, 1967; Shapiro, 1995).

#### ***Alouatta*, *Lagothrix***

The morphological results for *Alouatta* are quite interesting from a functional perspective. *Alouatta* is similar to other atelines in its transverse processes and vertebral body heights, but clearly resembles *Cebus* rather than the other atelines in lumbar vertebral body and region length (see also Erikson, 1963; Filler, 1986; Kelley, 1986). Behaviorally, *Alouatta* falls between *Ateles* and *Cebus* with respect to all of the behaviors that bring about predominantly ventrodorsal bending loads. Therefore, one might

expect *Alouatta*'s lumbar length to be intermediate between *Ateles* and *Cebus* as well. However, similarity in lumbar length between *Alouatta* and *Cebus* corresponds with their similar frequencies of quadrupedal locomotion. They are both more frequently quadrupedal than either *Ateles* or *Saimiri*. The relative elongation of the lumbar region in *Alouatta* and *Cebus* compared to *Ateles* and *Brachyteles* likely provides more flexibility during quadrupedal walking and running. On the other hand, the reduction in lumbar length of *Alouatta* and *Cebus* compared to *Saimiri* may be attributable to the former two species' higher frequencies of bending 1 loads, brought about for the most part by bridging behavior.

*Lagothrix*'s intermediate position in lumbar region length and slightly shortened vertebral bodies suggest its positional behavior induces reduced bending loads compared to *Ateles*, but perhaps slightly higher loads compared to *Alouatta*. Very little is known about the positional behavior of *Lagothrix*. Its behavior does appear to be somewhat intermediate between that of *Ateles/Brachyteles* and *Alouatta*. *Lagothrix* apparently utilizes quadrupedalism more frequently than does *Ateles* and suspensory behaviors/arm-swinging more frequently than *Alouatta* (Stern, 1971; Cant et al., 1996).

Preliminary observations indicate that the spinous processes of *Lagothrix* and *Alouatta* are more cranially oriented than those of *Ateles* and *Brachyteles*, but less than those of *Cebus* or *Saimiri* (see also Ankel, 1962). In other vertebral features examined here (i.e., vertebral body height and transverse process orientation), *Lagothrix* resembles all other atelines, indicating that it possesses a basic "ateline" vertebral adaptation.

#### ***Cebus*, *Saimiri***

The relatively reduced vertebral body height in *Cebus* compared to the larger bodied atelines is a function of positive allometry, i.e. a function of smaller body size possibly in conjunction with the lower frequency of bending 1 loads in *Cebus*. The more ventrally oriented transverse processes and narrower, more cranially oriented spinous processes (Ankel, 1962; per-

sonal observations) in *Cebus* reflect an increased erector spinae muscle mass (Benton, 1967) and more of an emphasis on sagittal flexibility (Rockwell et al., 1938; Howell, 1965; Gambaryan, 1974), consistent with *Cebus*' agile form of quadrupedalism compared to the "deliberate" quadrupedalism of *Alouatta* (Rosenberger and Strier, 1989).

*Saimiri* differs morphologically from atelines as well from *Cebus*. Among these taxa, *Saimiri* has the most lumbar vertebrae, the relatively longest vertebral bodies, and the longest lumbar region. *Saimiri* also has the highest frequency of bending 2, brought about mostly by leaping. Lumbar anatomy in *Saimiri* is convergent with that of other primate leapers, at least those that leap from a pronograde position (cf. Shapiro, 1995). Presumably, a relatively long lumbar region increases the distance traveled during a leap by increasing the distance through which force is applied during acceleration for takeoff (Preuschoft et al., 1979; Hildebrand, 1988; Fleagle, 1988). The details of spinal biomechanics during leaping have not been well studied in primates, however (but see Hall-Craggs, 1965; Preuschoft et al., 1979, 1995).

Although we ascribed reduced loads to bending 2 as compared to bending 1, it can be argued that the initial phase of leaping would place very high bending loads on the spine. Nevertheless, because loading is reduced in smaller animals, *Saimiri* does not appear to require ventrodorsal elongation of vertebrae or reduction of the lumbar region to counteract bending loads brought about by leaping. Rather, *Saimiri*'s elongated lumbar vertebral bodies and lumbar region accentuate sagittal flexibility and its associated bending loads. Finally, the transverse processes of *Saimiri* are more acutely ventrally angled than those of all other taxa in the sample. *Saimiri* also appears to have the most cranially oriented spinous processes as well (personal observations). These two aspects of morphology correspond well with the increased erector spinae muscle mass and sagittal flexibility required by leaping, and are characteristic of other primate and nonprimate mammalian leapers (Hatt, 1932; Currey, 1984).

### The evolution of lumbar reduction

This study has demonstrated that compared to *Saimiri*, the lumbar region is relatively short in atelines as well as in *Cebus*. Lumbar reduction has evolved more than once among primates—in platyrrhines, as well as in hominoids, indrids, and to some extent, lorids (Schultz, 1961; Erikson, 1963; Benton, 1967, 1974; Cartmill and Milton, 1977; Jungers, 1984; Ward, 1993; Sanders, 1995; Shapiro, 1995). The specific vertebral form-function links documented here for platyrrhines can shed light on the evolution of lumbar reduction in other groups of primates.

Erikson (1963) proposed overhead suspensory locomotion (including brachiation) as the most significant correlate to lumbar reduction in platyrrhines. Indeed, in this study, *Ateles*, with the most reduced lumbar region, was the only species (of the four observed here) to engage in arm-swinging locomotion. Nevertheless, while Erikson noted the variation in lumbar length among the atelines, he categorized all of them as "brachiators" to distinguish them from "climbers" (including *Cebus* and *Saimiri*) and "springers." It is clear from this study, as well as those by others (Table 8), that *Alouatta* is not a brachiator, and that *Cebus* and *Saimiri* are distinct both behaviorally and morphologically (Erikson recognized that *Alouatta*, *Cebus*, and *Saimiri* "bridge" categories with respect to forelimb, but not vertebral anatomy). Therefore, although arm-swinging may be functionally associated with lumbar reduction in *Ateles* (and perhaps *Brachyteles* and *Lagothrix*), the reduction in lumbar length present in *Alouatta* and *Cebus* compared to *Saimiri* suggests that arm-swinging is not the only behavior associated with this vertebral adaptation.

Rose (1975) suggested that lumbar reduction is associated with maintaining habitual trunkal erectness (i.e. orthograde) during positional behaviors, especially for hominoids. However, he also noted that the proportions of vertebral bodies may be more closely linked functionally to bending than to compression, particularly for *Ateles*. The present study supports this hypothesis, be-

cause among atelines, lumbar reduction appears to be biomechanically linked with increased frequencies of behaviors that presumably induce ventrodorsal bending stress on the spine. These behaviors include arm-swinging (with tail), bridging, suspensory hanging, and general use of the prehensile tail.

Rose's (1975) observations, in conjunction with the results of this study, underscore the importance of considering the loads induced by particular behaviors or postures, rather than simply noting the behaviors or postures themselves when attempting to evaluate morphological adaptations (e.g. Stern and Oxnard, 1973). That is, orthograde postures, or locomotor behaviors during which the spine is orthograde, can place various mechanical demands on the back, including tension, compression, or bending. The type of load induced by orthograde is dependent on which limbs are being used for support, and/or the incorporation of the prehensile tail (a key component for atelines). In fact, our results demonstrate a link between lumbar reduction and orthograde behaviors that bring about bending (e.g. arm-swinging with tail use, suspensory postures with three or more limbs or two limbs and tail, bridging) but not orthograde behaviors that induce compression (e.g. bipedal stance or locomotion, climbing, upright sitting). Moreover, the four taxa in this behavioral study did not vary significantly in their frequencies of compression, nor was increased compression consistent with shorter lumbar regions.

Functional interpretations of lumbar reduction in *Ateles* and *Brachyteles* (and to a lesser extent, *Lagothrix*) can also shed light on vertebral form and function in *Hylobates*, the hominoid with which these platyrrhines most closely converge morphologically. Despite the fact that all four of these taxa incorporate arm-swinging in their locomotor repertoire, it is unlikely that arm-swinging per se is responsible for the reduction of their lumbar regions. That is, arm-swinging places different mechanical demands on the spine in gibbons than it does in these three atelines. *Ateles*, *Brachyteles*, and *Lagothrix* frequently incorporate the prehensile tail as a supporting "limb" during arm-swinging (Jenkins et al., 1978; Cant, 1986; Rosen-

berger and Strier, 1989; Cant et al., 1996), producing bending loads on the spine. Other frequent suspensory behaviors documented here for *Ateles* also act to increase bending stress on the spine. Gibbons, on the other hand, lack a tail, and are less likely to sustain pronounced bending stress on the spine during arm-swinging. However, Jungers (1984) emphasized hylobatids' use of bridging behaviors as a functional link to their reduced lumbar regions (and positively allometric thoracic regions), as Cartmill and Milton (1977) had noted with regard to lorids, atelines, and hominoids. Bridging is also a behavior that is likely to place bending stress on the spine, best resisted by a reduction in length. For example, *Alouatta* bridges more often and has a shorter lumbar region than the cebines, and a similar trend describes lumbar reduction in *Cebus* vs. *Saimiri*. Therefore, rather than shared behaviors, it is more likely shared loading patterns (i.e., bending) that account for morphological convergence between hylobatids and atelines. Bending may also be an important factor accounting for the reduction of the lumbar region among indrids, which engage in frequent upright as well as suspensory postures and movements (Shapiro, 1995).

Among primates, lumbar reduction is most pronounced in non-hylobatid hominoids, particularly in great apes (Benton, 1967; Ankel, 1972; Schultz, 1961; Jungers, 1984; Ward, 1993; Sanders and Bodenbender, 1994; Sanders, 1995; Ward, 1993). Jungers (1984) suggested that lumbar reduction may function to counter buckling of the vertebral column during vertical climbing, particularly in large-bodied hominoids. However, a link between vertical climbing and lumbar reduction cannot be applied to the platyrrhines in this study. The frequency of climbing activities did not differ significantly across the four species, whereas lumbar region length differed notably. In addition, climbing (like bipedalism) most likely entails net compressive forces on the vertebral column, a loading regime that did not differ significantly across the four species.

In conclusion, many previous hypotheses about lumbar reduction in primates have isolated particular aspects of diverse behav-

ioral repertoires that, when considered as a whole and in terms of loading patterns, correlate more closely with lumbar length. A general suite of locomotor and postural behaviors (including arm-swinging, bridging, suspensory hanging, and prehensile tail use) best explains the adaptations present in the vertebral column of the atelines and, to a lesser extent, *Cebus*. Combining the frequencies of these behaviors for each species demonstrates a consistent pattern of increasing suspensory activities and decreasing lumbar column length. The overall frequency of bending 1 sustained by these species also conforms to this pattern. Moreover, the "short-backed" atelines demonstrate how different behaviors can be linked to similar structures (e.g., use of the tail during arm-swinging and other behaviors in *Ateles* vs. bridging in *Alouatta*).

Finally, this study provides evidence relevant to the question of whether the most common behaviors are primarily responsible for shaping vertebral anatomy. The most frequent postural and locomotor behavior subcategories were the same for all four species ("nonsuspensory postures" and "quadrupedal cursorial locomotion," respectively). These results suggest that secondary behaviors (i.e., behaviors that are less frequent, but more stressful or hazardous) may be sufficient to account for interspecific variation in vertebral morphology.

#### ACKNOWLEDGMENTS

S.E.J. expresses his great appreciation to the Direccion General de Vida Silvestre and the Servicio de Parques Nacionales (Ministerio de Recursos Naturales, Energia y Minas) of Costa Rica for permission and assistance in conducting research at Corcovado. Thanks go to curators and staff of the following institutions for providing access to, and assistance with the skeletal collections in their care: Rijksmuseum van Natuurlijke Historie (Leiden), British Museum of Natural History, Field Museum of Natural History, United States National Museum of Natural History, American Museum of Natural History, Museum of Comparative Zoology (Harvard), and the Department of Anatomical Sciences, SUNY at Stony Brook. Thanks also to Claud Bramblett, Sharon Bramblett,

and Lawrence Gilbert for their support in the undertaking of this project, to Susan Ford for help with references, to William Jungers for statistical advice, to John Kappelman for access to AutoCad software, to Deborah Overdorff, Claud Bramblett, and William Sanders for helpful comments on earlier versions of this manuscript, and to the two reviewers for comments that improved the paper. The research presented here was supported in part by NSF grant BNS 8823083 and by a University of Texas University Fellowship to S.E.J.

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